CONTRACT REVIEW

BREEDING OBJECTIVES FOR MEAT ANIMALS: INTRODUCTION

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Definition of breeding objectives sets the direction of breeding programs. There is little use in going fast if the direction is wrong. The classical and 'economically rational' approach to setting breeding objectives tells us to ignore genetic parameters, such as heritability, when calculating economic weightings. This is because the value of achieving a given genetic change is taken as independent from the difficulty in achieving such change. Costs of running the breeding program are accounted for when designing the program, and genetic parameters are accounted for when we construct the selection indices, or 'total score systems', which are used to rank and select animals for breeding. This approach to selection is predicted to be quite robust when properly applied in simple production systems. However, it makes assumptions in two areas that can be important for meat production:

- It assumes that we know the genetic parameters (heritabilities, genetic correlations and phenotypic correlations) for all traits that are measured and/or of economic importance. However, this is often not the case in meat production systems, where it is extremely difficult to measure many of the traits of true importance, such as mature size, shape of the growth and feeding curves, and the patterns of tissue deposition. Such traits are often ignored when developing breeding objectives and yet their direct or indirect effect on profit can be large.
- It generally assumes that the biological interactions among traits are linear in nature. However, this is often not the case in meat production systems, where relationships can be complex, such as the effect of fatness on maternal ability and juvenile survival in heterogeneous environments. It is possible that relationships are neutral at the current levels of trait expression, but that with genetic change in selected traits thresholds are passed and/or relationships develop.

Biological modeling of production systems can be used to predict such changes. Thus in a practical sense, biological modeling can be used to help set breeding objectives – for example by predicting otherwise unforeseen deleterious effects of a given selection program.

Such modeling usually involves a mixture of mechanistic and empirical features. Mechanistic features give powers of extrapolation beyond what we get through use of empirically derived parameters such as heritabilities and linear correlations. However, biological modeling cannot be used to reliably separate predictions of genetic relationships and phenotypic relationships, and this casts doubt on its power to help set breeding objectives.

This contract presents both the economically rational view, usually presented by geneticists, and the biological modeling view, which might be put by researchers in growth and development. It is evident that each view is sensitive to the other, but that there is room to more fully integrate the approaches involved. In practice, biological modeling might play a quality control role, to predict any deleterious effects of breeding objectives set through use of an economically rational approach.

BREEDING OBJECTIVES FOR MEAT ANIMALS: DEVELOPMENT OF A PROFIT FUNCTION

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In the design of a breeding program one of the first tasks is to decide on a breeding objective. This is done by a profit function which describes how each trait affects profit. This is important because it tells us which

traits have most effect on profit and therefore deserve most emphasis in the breeding program. The profit function is used in several decisions which are crucial to the breeding program. For instance, it is used in comparing alternative breeds and crosses, selecting individual sires and dams as parents of the next generation or deciding whether investment in AI will be worthwhile. If the profit function is to be used for all these purposes it must be independent of how genetic change is achieved. That is, it evaluates the profit or loss from a genetic change without any reference to how this change is brought about. Consequently it must be phrased in terms of traits which directly determine income and costs even if these traits are hard to measure (eg feed intake).

  When selecting individual animals as parents we base our decisions on selection criteria. The traits included in the selection criteria need not be the same as those that are included in the breeding objective or profit function. For instance, food intake may be included in the profit function because it directly affects costs, but mature weight might be included in the selection criteria because it is easily measurable and correlated with food intake. There are well established methods for finding the selection criterion which is most highly correlated with the breeding objective. In this paper we will be concerned with defining the breeding objective and consider only briefly how to select for it. Barwick (1992) gives an overview which shows how the breeding objective can be targeted through use of a customised selection index.

  A detailed profit function for cattle would be different to one for meat sheep or pigs but there are traits which are important in all meat production. The main aim of this paper is to describe a generic profit function for meat producing species in an attempt to clarify the relative importance of key traits and their consequent weightings in a selection index. In addition, the potential to augment the selection index with information derived from biological modeling will be discussed.

A GENERIC PROFIT FUNCTION FOR MEAT ANIMALS
Assume the herd or flock is composed of two classes of animal – dams and slaughter stock.

Let: Profit   =   Income minus Costs
        Income   =   No. Dams * reproductive rate * $weight_s$ * % meat * price/kg meat
        Costs   =   Cost of feed for dams
                                     + cost of feed for slaughter stock
                                     + costs which are proportional to no. of dams
                                     + costs which are proportional to no. of slaughter stock
                            =   No. of dams * $weight_D^{0.75}$ * FCR_D
                                     + no. of dams * reproductive rate * $weight_s$ * FCR_s
                                     + no. of dams * cost/dam
                                     + no. of dams * reproductive rate * cost/slaughter animal

where: Reproductive rate   =   no. of young per dam-year less deaths of dam or young
        % meat   =   proportion of sale weight which is retail meat
        $weight_s$ =   weight of slaughter stock at sale
        price/kg meat   =   average price received per kg retail meat
        No. of dams   =   number of dams mated each year
        $weight_D$ =   weight of dams
        FCR_D =   food required for maintenance of dams in $ per unit of metabolic live
                                     weight
        FCR_s =   food required per kg live weight gain in slaughter stock
        cost/dam   =   annual cost other than feed per dam
        cost/slaughter animal = cost other than feed per slaughter offspring from birth to slaughter

  A term which has been left out of the formula for profit is [income from sale of cull dams minus the cost of rearing or buying replacement dams]. We will assume for the present exercise that these two terms roughly cancel each other out and ignore them.

The definition of costs does not include fixed costs because we assume that, in the long term when farm management is optimised, all costs are proportional to either the feed required or the number of animals. For instance, the capital cost of a piggery depends on the number of pigs it will house; the cost of buying and running grazing land is a feed cost because, with optimised management, the total amount of feed grown is limited by the amount of land.

In general we expect profit to be close to zero after returns to capital, management and labour have been counted as costs. Thus income is approximately equal to costs.

ECONOMIC VALUES

From the profit function we can calculate the economic value for each trait, ie the amount by which profit increases due to a one unit increase in that trait, while all other traits are held constant. Table 1 gives the economic values for a 1% increase in each trait in terms of three key parameters: costs for slaughter animals (ie no. of dams * reproductive rate * cost/ slaughter animal), feed costs for slaughter animals (no. of dams * reproductive rate * weight$_s$ * FCR$_s$) and feed costs for dams (no. of dams * weight$_D$$^{0.75}$ * FCR$_D$), all expressed as a proportion of total costs or income.

Table 1 shows that a 1% increase in reproductive rate causes an increase in profit which is equal to $(1-a_s-f_s)$% of income. This is because the income is increased by 1% but there are more slaughter animals and so feed costs and other costs proportional to the number of slaughter animals also increase. Consequently if most costs (feed and other) are due to slaughter animals the economic benefit from increasing reproductive rate are not great. This might occur if reproductive rate is already high so that the number of slaughter animals is high relative to the number of dams (eg in poultry). Conversely if most costs are associated with dams, the benefit of increasing reproductive rate is high (eg vealer production in beef cattle).

Table 1 shows that a 1% increase in sale weight is worth $(1-f_s)$% of income increase in profit even if FCR$_s$ remains unchanged. That is, if the feed costs for slaughter stock are low the economic value of increasing sale weight is high. However, if the feed costs of slaughter animals (f_s) are high, as in pig production, the value of increasing sale weight is low and it is more valuable to decrease FCR$_s$. (Note that the economic weight of FCR$_s$ is very simple, it is just the proportion of all costs, or income, which is attributable to feeding slaughter animals, and the negative sign means that increasing FCR$_s$ decreases profit).

Table 1 can also be used to calculate the value of changing two traits together. For instance, if both the sale weight and the weight of dams are increased by 1% then the benefit is $(1-f_s-0.75 f_d)$% of income. Thus increasing both weights by 1% is of some benefit because dam feed costs only increase 0.75% and other costs which are proportional to numbers of animals do not increase. Nevertheless, if most costs are feed costs, the economic benefit might still be small.

The use of a single trait called price of meat/kg does not imply that this is the same trait for all producers. For instance, a pig producer may get a premium for leanness but a sheep producer for heavy carcasses. Even within a species the factors affecting price of meat/kg will vary thus changing the definition of the objective.

Table 1. The value of a 1% change in each trait expressed as a percentage of gross income

Trait	Economic weight (% value / % change)	CV$_g$ (%)
Reproductive rate	$1 - a_s - f_s$	4-14
Weight$_s$	$1 - f_s$	7
% meat	1	3
Price of meat/kg	1	6
Weight$_D$	$-0.75 f_d$	7
FCR$_D$	$-f_d$	8
FCR$_S$	$-f_s$	8
Cost/dam	$-(1-a_y-f_d-f_s)$	?
Cost/slaughter animal	$-a_y$	?

a_s = slaughter animal costs as a proportion of income
f_s = feed costs for slaughter stock as a proportion of income
f_d = feed costs for dams as a proportion of income
CV_g = genetic coefficient of variation

In general, each individual producer will have a slightly different breeding objective depending on his environment, production system, target market and the merit of his current herd or flock.

The objective proposed is an economic one but it would be possible to add other outcomes to it such as the welfare of the animals and the environment. The breeding objective we have used assumes that the total amount of feed harvested from the farm cannot be increased by a genetic change in the animals. This provides some protection against seeking genetic changes which lead to overgrazing.

WHOSE PERSPECTIVE DETERMINES THE OBJECTIVE?

Should the breeding objective be defined from the perspective of the individual producer, the industry, or society as a whole? Fortunately the objective is the same from all perspectives provided that average profit is close to zero and price signals are passed up the production chain from consumer to seedstock breeder. The latter does not always occur. For instance, producers are not usually paid on the basis of kg of retail meat but on kg of live weight or carcass weight. The trend is for market price to more closely reflect the value of the meat or carcass to the buyer (value based trading) so we expect that market signals will be more effectively passed back to the producer and seedstock breeder in the future. Since genetic change is a long term benefit, it is reasonable to base one's breeding objective on likely future payment systems. In the meantime, the objective proposed represents that of the industry or of a vertically integrated producer.

HOW MUCH IMPROVEMENT IS POSSIBLE?

The economic values in Table 1 are for a 1% increase in each trait. However some traits are less variable and therefore harder to change than others. Table 1 also contains typical values for the genetic standard deviation of each trait expressed as a percentage of the mean.

Thus the economic value of percent meat is high but the amount of variation in this trait is lower than that of most traits. The genetic variation in price of meat/kg is highly dependent on the traits that determine price and the extent of the premiums or penalties paid. For instance, in the Japanese beef market the premiums for marbling are high and there is good genetic variation in marbling, so the genetic variance in price of meat/kg is high (this is the value given in Table 1), but for other situations the genetic variance may be much lower. Considering both the economic values and the genetic variances, it is usually found that at least the first seven traits in Table 1 are all important.

It is possible that a trait in the objective cannot be improved because it is controlled by other traits which are already at their optimum values. For instance, price/kg of meat may be dependent on carcass weight and fat depth with both overweight, underweight, overfat and underfat carcasses being penalised. In this situation once the animals are at the optimum weight and fat depth no further improvement in price/kg of meat is possible. When such optima occur it is important to be able to predict the actual performance of slaughter animals so that the breeding stock that will produce slaughter descendants closest to the optimum can be selected. However it is unusual that there is no possible improvement in one of the nine traits in the breeding objective. By focusing on these nine traits we focus on where improvements can be made, rather than focusing on traits which are already close to optimum.

The progress that can be made in improving profit also depends on the genetic correlations between traits. Unfavourable genetic correlations reduce the amount of progress possible. For instance, fatter animals tend to have a reduced percentage meat but increased marbling (intra-muscular fat) creating a negative and unfavourable correlation between percent meat and price of meat/kg for the Japanese beef market. However based on some evidence in the Angus breed (Wilson *et al*. 1993) the genetic correlation is not strong, so it is quite possible to find sires which increase both percent meat and price of meat/kg.

The genetic correlation between sale weight and dam weight in cattle is approximately 0.7 (Koots *et al.* 1994) and therefore unfavourable. However it is not 1.0 so it is possible to select for cattle whose 18 month weight is high relative to their mature cow weight.

This example illustrates the importance of the precise way in which selection is carried out. Selection for sale weight will increase it proportionately more than mature cow weight which is a beneficial change in the shape of the growth curve. However selection for mature cow weight will increase it proportionately more than sale weight. If frame score is highly correlated with mature cow weight, selection for frame score will also cause an unfavourable change in the shape of the growth curve.

Sometimes genetic correlations are favourable. For instance, increasing percent meat by decreasing fat deposition may also decrease FCR_s and hence decrease feed costs.

Since so many traits are important to profit and often correlated with one another, it is important to choose a selection criterion which takes economic values, variances and correlations into account. A selection index is the best way to do this (Barwick 1992). A selection index, if calculated correctly, selects the animals which will produce the most profitable offspring.

The genetic correlations among these traits are crucial information in deciding how to select for improvement in profit, but there are still many genetic correlations that we do not know.

HOW RELIABLE IS THE SELECTION INDEX?

The selection index accommodates correlations among the traits that have been identified as either objective traits or criterion traits. If this information is complete and reliable, and the relationship among traits is reasonably linear, then the selection index will give genetic change about as predicted by theory.

However there are often traits that should be included in the breeding objective (eg life history fitness traits) whose correlations with other traits are rarely if ever estimated in domestic species. In the absence of such estimates, it is tempting to speculate based on biological considerations. For example:

- Selection for reduced fatness may lead to reduced fertility and increased post-natal mortality in stressful environments, due to reduced energy reserves for pregnancy and lactation. This seems reasonable through simple logic even though it is difficult to establish experimentally.

- Bos indicus cattle have a lower maintenance requirement and a lower growth rate in a favourable environment than do Bos taurus cattle. From this we might expect selection for growth rate to cause an increase in FCR_D.

- Patterns across species suggest that animals that grow faster to a larger mature size will reach puberty at a later stage. Thus selection for mature size may reduce production efficiency due to the need to hold breeding females for an extra year. However selection for growth rate leads to earlier puberty especially among Bos indicus cattle in the tropics – illustrating that great care must be taken in formulating policy from breed or species comparisons.

Predicting relationships between traits based on our knowledge of the biology and observed patterns across species is potentially powerful because of the lack of constraint to the fixed age and weight measures we routinely take, and the power to make inference outside the genetic and environmental limits of the data we use to estimate simple genetic correlations. However, great caution is required here because breed differences are not a reliable guide to within breed genetic correlations. There is no substitute for direct estimation of the relevant genetic correlations wherever this can be done, with monitoring for any unexpected correlated responses to selection and updated correlation estimates as genetic change is made.

BREEDING OBJECTIVES FOR MEAT ANIMALS: USE OF BIOLOGICAL MODELING

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Historically, selection objectives for meat producing species have focused on maximising output. However, more recently efficiency of production and increased emphasis on meat quality have become the key criteria. This increases the need for knowledge about the relationships between production traits, efficiency and meat quality.

In most cases, the study of phenotypic and genetic correlations among these traits suffers from the narrow width and fixed-stage recording of the simple traits measured. This limits prediction of correlated effects to presumed linear associations based on sometimes inappropriate animal measurements. On the other hand, biological modeling of growth and efficiency traits, together with calibration through comprehensive recording of key traits over time, can lead to a much more robust framework to predict the full consequences of phenotypic change in objective traits. The weakness of the latter approach is the great difficulty in finding

genetic relationships rather than phenotypic relationships. These issues are of practical importance in setting breeding objectives, wherever the available genetic parameters cannot provide confident predictions of the complex biological changes that can result from selection.

This paper attempts to contribute to discussion on breeding objectives for meat production, through use of biological understanding of growth and development to predict the correlated effects of selection on key criteria.

MODELS FOR GROWTH

Modeling animal growth can be undertaken at a number of levels. The majority of models are mechanistic, although several have been developed from the mechanistic to the stochastic.

Simple models

The first level of modeling is to simply obtain empirical relationships between parameters and then use these to consider the consequences of genetic or environmental change in one of the parameters on another. This approach does not assume any underlying biological relationships and there is often little confidence in the transportability of the relationship to other environments, or genetic pools. In essence this is the approach taken with obtaining genetic covariances, which assume a linear relationship. In addition to the problem of transportability this approach is further limited in that the confidence in the response is restricted to the traits that are currently being measured. If all traits are being measured on immature animals there is little confidence in the response in other traits such as mature food intake. A further problem is that traits are often measured over time are often these traits are treated as separate, when in actual fact they are part of the same biological complex.

The next level of modeling is to develop input/output models, where functions based on some underlying biological principle are used. These models can range in complexity from the simple input/output functions used by Parks (1982) to the more complex models, such as are used by Black (1986). The parameters which drive these models can be considered as sub traits which are functions of the models hypothesised. These sub-traits are somewhat abstract, being, for example, mathematical components of a growth curve rather than levels of a given enzyme. As with most of the growth models the underlying assumption is that growth over an extended period is non-linear. The interpretation of the sub-traits is often difficult as they often relate to exponential rates of change, rather than traits that can be easily measured in the field.

In the case of the Parks models there is a parameter called t* which can be interpreted as an appetance factor. It can only be estimated using the non-linear model proposed by Parks and it is sometimes difficult to relate to the more traditional measurements of daily food intake. The efficiency parameter (AB) is somewhat more complex in that it is a measure of true food efficiency that is adjusted for the body weight or maintenance component of the animal. In effect the term (AB) can be thought of as the net summation of the processes of digestion, absorption and utilisation of nutrients in the body. However it cannot be directly related to more conventional measurements of any of these three processes. There is generally little genetic information available for these construed sub-traits as the long term nature of the experiments to derive the parameters is prohibitively expensive. Parratt (1983) and Stephens (1991) showed that using mice many of the growth modeling traits had reasonable heritabilities, although there are no estimates for the larger species.

The input/output models can vary greatly in complexity. The Parks approach was to simply take a 'black box' approach and the magnitude of the parameters was confounded by genetic and environmental factors. This necessitated that the parameters were derived empirically for each genotype and environment combination and consequently there was little transportability in the parameters between populations or environments.

Other models such as nationally recognized feeding standards are much more detailed and there is an attempt to partition out the various mechanisms that contribute to growth and development of the body tissues. These more detailed functions have been extracted from experiments and then incorporated into the model. This limits the ability to test for extreme conditions and interactions that are outside the scope of these initial experiments. However in a controlled environments these models do accurately predict the outputs.

Dynamic systems modeling

Dynamic systems modeling would appear to be to the next level of modelling that is developing for use in the

animal growth area. (Oddy *et al.* 1997). The first step is an analysis of the system as a time series. From this a conceptual model that describes the behavior of the system is formulated which captures the biology in mathematical terms. The advantage of this system is that it allows animals to deviate from the 'normal' growth pattern and retain the capacity to return by a different trajectory. Therefore it is capable of capturing both the current status of the animal and its future potential as influenced by past events. The level of abstraction is generally to the level that you can reliably measure, although the mathematical forms are set by understanding the levels (biology) underneath.

Modeling from the molecular level.

A group of future developments that must be currently considered in the science fiction category relate to building biological models of gene action and interaction - models that have the power to predict ideal genotypes across many loci. This is quite different from the current wide use of biometrical models to predict genetic values - biological modeling provides a *mechanistic* prediction of ideal genotypes across loci, not an empirical extrapolation, which is typical of classical breeding objective and genetic evaluation calculations.

As quantitative trait loci (QTL) become identified at an increasing rate, there is the basis for an escalation of information on gene action and interaction. This will help with the modeling of biochemical pathways, hormone-receptor interactions, etc. However, epistasis and homeostasis will make such modeling of life processes very complex indeed.

Nevertheless, there is and will be activity in this area. Recombinant DNA will be used to generate key genotypes which provide information for modeling. A recent development here is the generation of viable animals following nuclear transfer from populations of cells maintained *in vitro*, giving a route to extensive transgenic work (Campbell *et al.* 1996). In addition, the use of *in vitro* meiosis (IVM), if developed, together with selection at known QTL to generate suites of test genotypes would play an important role. One can imagine targeting the generation through IVM selection of a suite of nominated genotypes across loci, to be raised to the age(s) of trait expression, and used to help develop and test biological models of gene action and interaction. With many QTL cloned, this approach could be used iteratively to build biological models of gene action. However, any such developments are not likely to occur for some considerable time.

MODELING AT THE ENTERPRISE LEVEL

Parks (1982) took a simplistic approach to the problem treating animal growth as a simple input/output function. His early functions were confined to describing the changes in body weight as a function of feed inputs. Genetic (ie due to species or breeds) and environmental (ie protein and energy content of the ration) effects were incorporated in the coefficients of the input/output functions. As mentioned the interpretation of these coefficients was often difficult. However these models did have the advantage of accurately describing the pattern of food intake and live weight change for individual animals. These functions were then used by Thompson and Barlow (1986) as a basis for developing a model for biological efficiency of the dam/offspring enterprise. These models allowed a sensitivity analysis as to the effect of change (whether genetic or environmental) of particular parameters on biological efficiency of the enterprise. Their analysis showed that for a system with a relatively low reproduction rate the greatest gain in biological efficiency was obtained by an increase in maintenance efficiency. In contrast changes in the efficiency of converting food into live weight had a much smaller effect on biological efficiency. The results also showed that the appetance parameter, which was most likely to be responsive to selection pressure, was likely to have the least effect on biological efficiency at the enterprise level.

An example of where the modeling approach has been used to predict a correlated response in efficiency to selection for low backfat was given by Ball and Thompson (1995). Selection for leanness produces a commercially more valuable product but since leanness was positively correlated with higher maintenance costs the net effect on efficiency at the enterprise level was not clear. The higher maintenance costs in leaner sheep have been attributed to higher costs associated with protein turnover, both in the carcass and more importantly in the visceral organs. At immature market weights the effects of increased leanness may have little effect on growth efficiency, although if selection for leanness leads to a correlated response in mature females this could have a dramatic effect on enterprise efficiency.

Data from several experiments were used to estimate the parameters for the model. These included changes in mature maintenance efficiency and body composition. The results showed that the biological efficiency was responsive to changes in mature food intake, but any adverse effects of increased maintenance costs by

selection for leaner sheep was more than outweighed by the increase in biological efficiency by production of more lean tissue. The model was capable of integrating changes in both maintenance efficiency and body composition to estimate a net change in biological efficiency. The limitation to this system is that it assumes knowledge of the mechanism by which the biological change takes in place in the animal. These are simply based on phenotypic relationships that have been observed and in theory changes could be effected by either nutritional or genetic means.

The traditional selection theory approach at least partitions relationships into genetic and environmental components, but provides no framework as to how these can be used, other than is a simple linear fashion.

CONCLUSION

This contract has presented two views on setting breeding objectives for meat animals: economically rational, and biological.

In the economically rational view, a simplified breeding objective covering all meat producing species is described using only nine traits. The economic values for these traits depend only on the proportion of costs due to dams and slaughter stock and the proportion of each which are feed costs. In most circumstances reproductive rate, growth rate, carcass value and food conversion ratio are all important and deserve to be included in practical breeding objectives. There are many correlations between these traits, some of which are unfavourable and some of which we know little about. Consequently seemingly similar selection criteria (eg growth rate vs frame score) can have quite different effects on profitability. Therefore it is important to take account of both the economic weights and the variances and correlations among traits when deciding on a selection criterion. A selection index is the logical way to do this. The reliability of selection indices is discussed in relation to complex traits that might not be fully accommodated.

Biological modeling promises in the long term to offer a much more flexible and realistic framework to predicting the *full* impact of genetic changes in the simple traits that are typically included in breeding objectives for meat production. However, the currently used models suffer from a lack of ability to distinguish any differential impacts of environmentally versus genetically induced change – a problem which should be at least partly overcome with the development and use of progressively more dynamic and mechanistic models. In addition, simple biological models *per se* do not use the full population information available, where for example genetic correlations might differ considerably between two otherwise similar scenarios. At this stage, the optimal route in defining breeding objectives is probably to use biological modeling as a quality control to warn of otherwise unpredicted effects in breeding programs, and consequently as a possible modifier of objectives calculated by the economically rational approach.

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